Observations on the Behavior of *Xylocopa c. californica* and *X. tabaniformis orpifex*

(Hymenoptera : Apoidea)

Robert William Cruden
Department of Botany, University of California, Berkeley

Below I describe and interpret the behavior of the carpenter bee, *Xylocopa californica californica* Cresson, and comment briefly on *X. tabaniformis orpifex* Smith. The little that is known concerning the behavior of these bees can be found in the studies of Hurd (1958), Hurd and Moure (1963), Janzen (1964), and O'Brien and Hurd (1965). I have included a description and illustrations of the primary study area to provide orientation.

The two species of bees nest in redwood timbers and paneling in several buildings in the ghost town, Allen Springs. This town is located on Bartlett Creek between Bartlett Springs and Hough Springs in Lake County, California. The original building, a hotel, was constructed in 1876. In the late 1940's a series of houses were constructed across the road from the hotel. These buildings, including the hotel, were in use through the late 1950's. Visitors to the hotel in the late 1940's recall the presence of bees around the hotel porch and occupants of the houses remember the noise of bees burrowing in the paneling. It seems likely the original colony was located in the hotel and the colonies in the various houses are of later origin.

The hotel porch (Fig. 1) was the major study area as it was easily observed from all sides and allowed close observation of the bees. Fig. 2 shows the physical plan of the porch roof supports. The numbers indicate the position of hovering males of *X. c. californica* on 20 June 1965. Also indicated are the positions of various nest entrances into which bees, both male and female, were observed to go. Only one-fourth of the porch is now standing, the remainder has collapsed. The standing portion is 9 feet deep and 8 feet across the front and the second story is 9½ feet above the ground. The basic support for the porch roof is a series of seven 2×8-inch planks set edgewise on 7¾-inch square timbers. The vertical supports, set on stone and concrete pillars, are also 7¾-inch timbers. The bees nest in these various planks and timbers, both standing and fallen.

Xylocopa californica californica

Territories.—Territories of *X. c. californica* were recognized by the presence of hovering males and the aggressive behavior directed at

The Pan-Pacific Entomologist 42: 111–119. April 1966

Fig. 1. View of hotel porch at Allen Springs from northwest. Fallen portion of porch to right.

other *X. c. californica* males that approached a hovering male. Aggressive behavior was also elicited by various Diptera, Lepidoptera, other Hymenoptera (with the exception of *X. t. orpifex*), and even a hummingbird.

On 9 May, 13 territories, and on 20 June, 15 territories were defended. The increase was the result of two territories being abandoned and four new territories being defended. On 20 June, eight territories were located along the periphery of the porch roof, four were beneath the porch roof, and three (13–15) were in front of various fallen timbers, including one territory (14) located beneath a fallen portion of the porch roof.

Within a territory a male had a focal point, namely the entrance(s) to a nest. During periods of great activity the males hovered 2 to 10 inches from the nest entrance. A constant position was maintained in front of and facing the entrance. The distance from the nest was inversely proportional to the number of males present and the number of intrusions into the territory at any given time. At times of maximum and minimum activity the territorial boundaries became vague although the focal point remained. At times of maximum activity there were so many intrusions into a territory that it was impossible to determine the current defender from the challengers. Indeed, the area around

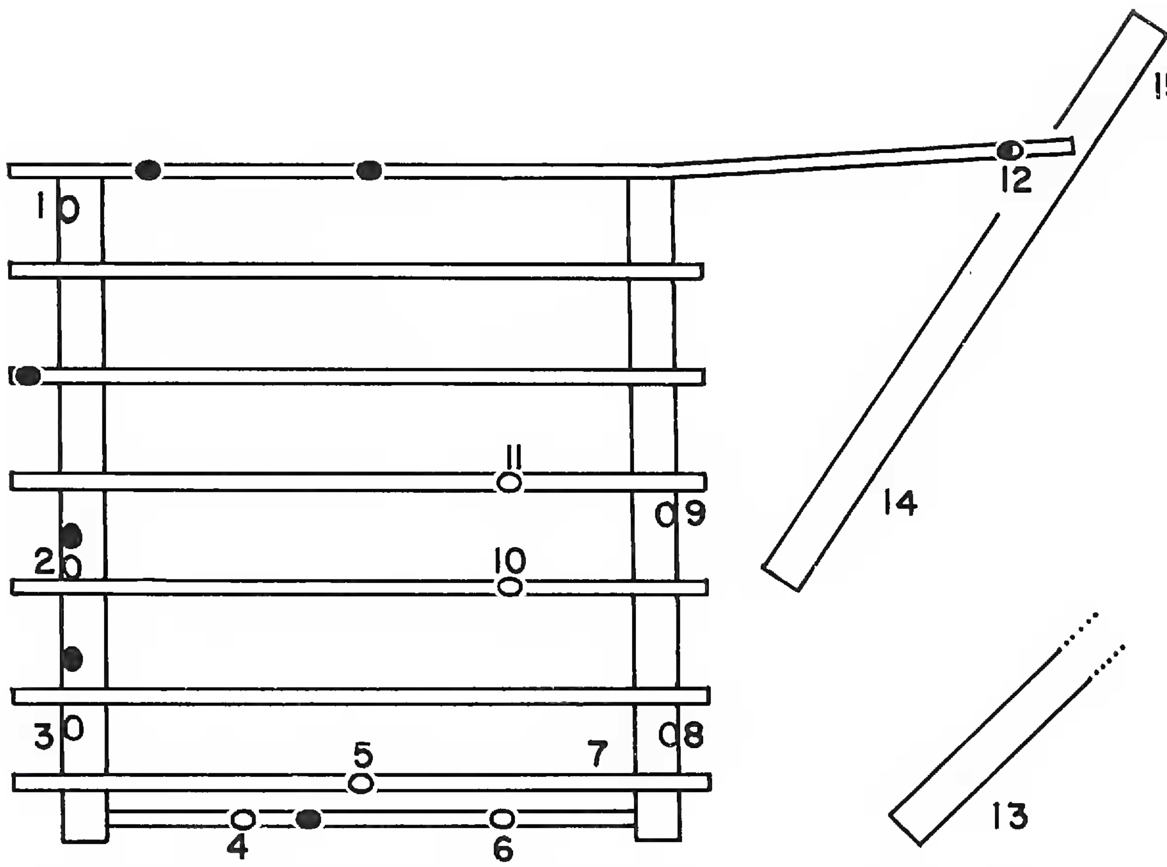

Fig. 2. Diagram of timbers and planks supporting porch as viewed from above. Fallen portion of porch to right. (See text for details.) Open oval indicates nest entrance of *Xylocopa c. californica*. Solid oval indicates nest entrance of *X. tabaniformis orpifex*.

and including the territory at times was filled with swarming bees. At times of minimal activity, a male in a territory hovered for a few minutes, then flew to nearby territories as if to find another bee to chase. During periods of decreased activity males hovered as much as 2 feet from the nest entrances.

Intrusion of a male into, through, or close to a territory elicited one of three distinct responses. The first was a simple chasing of the invader with a rapid return to the nest area. Second was a circling of the two males, with some body contact followed by a chase and rapid return to the territory. Usually such encounters were rapid and the bees did not rise much above the point of contact. Third, there was a towering flight of several hundred feet into the air, preceded by a circling flight. The first behavioral pattern is directed towards aggressors of the same species or other organisms that inadvertently fly through or near the territory. The second and third patterns are in response to aggressors that direct their flight toward the hovering male, including attempts to grasp the defender in a copulatory position. In the latter two patterns the attacker often came from above and behind the hovering male. On 22 May, a day of decreased male activity, type III encounters removed the bees from a territory for well over 10 minutes. This is probably significant, because on a day of great activity only 2 to 4 minutes elapsed before a new male moved into a territory from which the original male had been artificially removed.

On 9 May and 20 June, days of intense male activity, such towering flights occurred. If the combatants were away from the nest for long periods of time a new male undoubtedly occupied the territory before the defender returned. This provides an opportunity for each female in a nest to mate with a different male, rather than each female in a nest mating with the same male. Whether or not this is a built-in behavioral mechanism, it does assure, in Allen Springs at least, a greater number of possible genic recombinations, in contrast to the extreme model in which only a single male might fertilize all the females in a given nest. The chasing patterns do not remove a male from the territory for a sufficiently long enough period of time for him to be replaced. Males may also lose their territories when they visit flowers for nectar. The towering flights following copulation also remove the males from the territory for long periods of time.

Of particular interest during hovering was "leg dangling." This behavior seemed in some cases to precede the intrusion of another bee into the territory. In other cases the male dangled his legs repeatedly while hovering with no subsequent change in behavior. Leg dangling consisted of the legs more or less dangling loosely below the bee, rather than being tucked up along the sides of the abdomen as they usually are, and rubbing the tarsi together so that the red–brown hairs on the inside of the tarsi were clearly visible from behind, especially if caught in the sunlight.

As indicated above, males were artificially removed from their territories. A new male occupied the territory in a matter of 2 to 4 minutes. The male that eventually took over the territory first hovered at the edge of the territory displaced from the nest hole by some 6 to 12 inches. This behavior seemed to anticipate the momentary return of the previous occupant. Very quickly the new occupant moved to a position in front of the nest entrance and assumed the character of the defender. When released, the former occupant, in two of three cases, flew directly to the nest entrance where the usual behavioral pattern of circle and chase was enacted. It was not possible to tell which bee had prevailed as the bees were unmarked.

At times of intermediate activity, as on 20 June, when not too many intrusions were made into a territory, males repeatedly landed on the beams and planks and rested for upwards of 30 to 60 seconds. During this time they brushed their hind legs over their abdomens and cleaned their antennae.

COPULATORY BEHAVIOR.—On 9 May and 20 June two mating patterns were observed. The second type is probably a modification of the first. On the earlier date males and females were observed to fall onto the ground where copulation probably occurred. At this time I was unable to determine from whence came the females, but they were pursued and pushed towards the ground by repeated advances of one or two pursuing males. In each case on this day the female was pursued by two males, one of which did not engage the female. Very quickly the female was forced to the ground where the male was able to secure a position on her back. Copulation probably occurred during the 30 to 90 seconds on the ground. Then the bees suddenly broke apart with the female rising above the two males and facing them. The three bees occupied radii on a circle some 120° apart. The female flew backwards, closely followed by the males, to heights of over a hundred feet. On several occasions the bees passed from sight, even when viewed with seven-power field glasses. Nothing in this soaring flight indicated that copulation occurred at this time although one or both of the males might make head-to-head contact with the female.

On 20 June only once did I observe the above pattern. In this instance the female flew with a slow hovering flight toward the porch where a male pounced on her, she dropped about 3 feet, and the pattern repeated with the two bees quickly ending up on the ground. From nowhere it seemed a second male joined the pair but did not contact them. Almost immediately the three rose into the air and flew over the porch with the female flying backwards as described above. As the trio passed over the porch the attending male returned to one of the nest areas. Almost immediately the female turned and flew directly away from the following male and toward a nearby tree. Immediately the following male pounced on her back. Twice during the few seconds it took the female to reach the tree the male had made physical contact with her. The female landed on a limb and the male returned to the area of the porch.

The other male–female interactions were much less spectacular. In each case the female approached the porch with a hesitant, hovering flight. After approaching a female, the male either hovered in front of and below her or returned quickly to his territory with no further response. When the male hovered in front of the female she either failed to respond or reacted with a backing-up flight. The latter usually caused the male to return to his territory. From the hovering position in front of the female, the male quickly gained a position above and behind the female, made contact with her, and returned to his position in front and below her. Whether copulation actually took place during these contacts is not known. After each such interaction the female dropped a few feet and slowly recovered her former position. There seemed to be no attempt on the part of these females to avoid contact with the males. Such interactions occurred as many as four or five times between the same individuals in a period of a minute or two. Pollen-laden females returning to the nest flew with the same slow hovering flight but rarely elicited responses from the males. When males made aggressive advances towards these females they rose slightly and the male usually returned to his hovering position in front of a nest.

Attempted mating, at least, is not restricted to the nest areas. At Allen Springs a male was observed to pounce on a female that was taking nectar from the flowers of the milkweed, *Asclepias speciosa* Torr. This male made several passes at the female and made physical contact on at least two of these passes. After the first advance the male backed away and hovered for a moment or two before pouncing on her a second time.

Males of *X. c. californica* patrolled through and around the milkweed plants in the same manner that males of various solitary bees do when looking for females. This same patrolling behavior was noted around plants of *Lupinus* sp. and *Penstemon breviflorus* Lindl. in Yosemite National Park. The latter plant was a nectar source for at least the females in Yosemite. The milkweed served as a nectar source for both males and females at Allen Springs.

TIME OF ACTIVITY.—Fig. 3 shows the degree of hovering activity and the time of mating activity during the periods of observation with the exception of a visit on 4 August from 0700 to 1400 hours. On 4 August only two or three males were observed around the nest sites and their behavior was similar to that described for periods of low male concentration. No mating was observed on this date. Owing to the cloudiness, the hovering activity decreased on 22 May. The times given are in Pacific Standard Time.

Hurd (1958) reports hovering activity of *X. c. arizonensis* Cresson males for the few hours around noon and in the early afternoon. Hurd's information and my observation on 24 April and 9 May (see Fig. 3) suggested: (1) a limited period of mating activity during the day, and (2) that the daily hovering period decreased, during the season, to

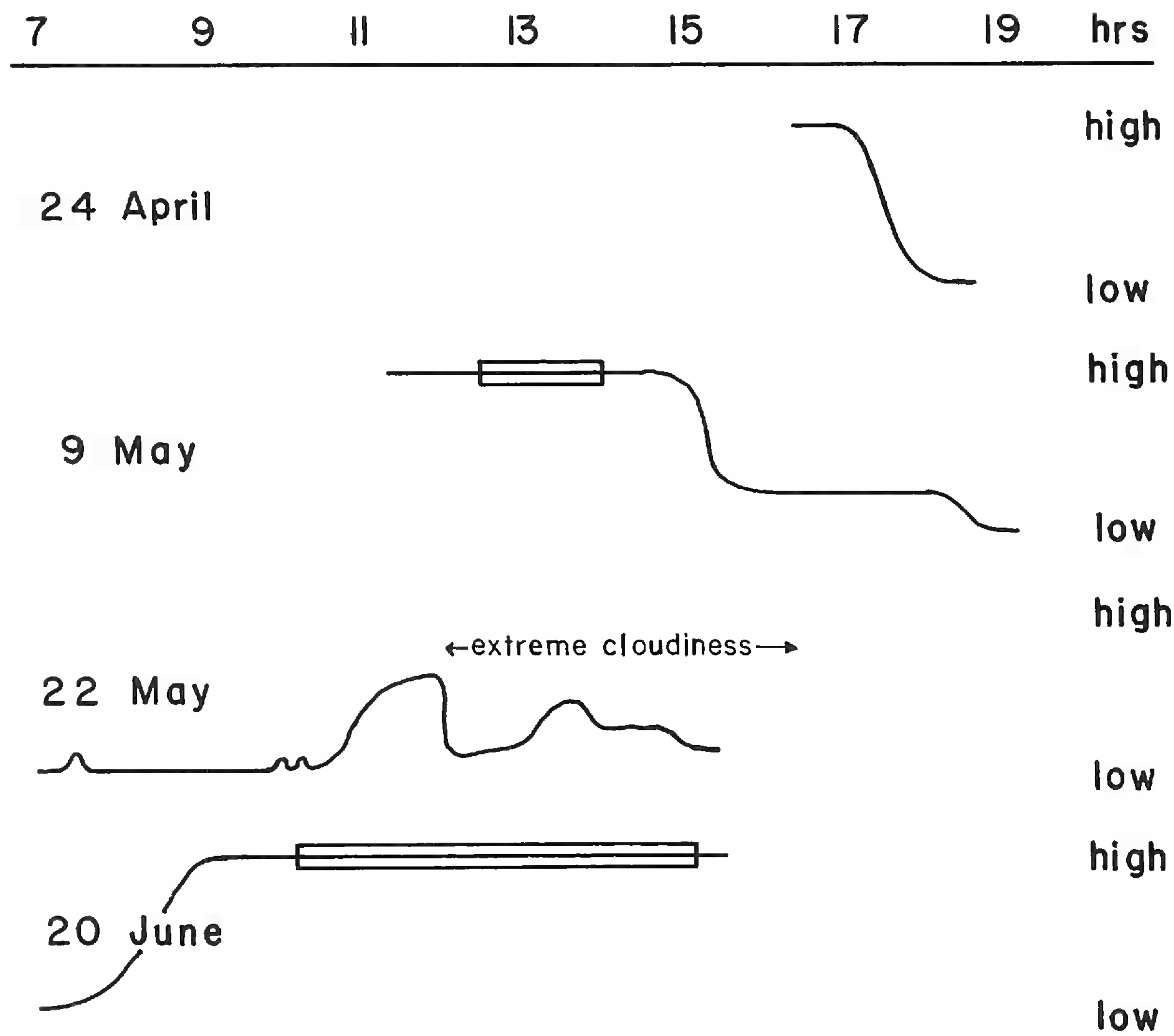

Fig. 3. Hovering activity of *Xylocopa c. californica* males and mating activity during periods of observation at Allen Springs. (See text for details.) Narrow line indicates degree of male hovering activity. Bar indicates mating activity.

more or less coincide with the daily mating period. However, my observations of 20 June seem to negate this idea. On this latter date (see Fig. 3) hovering activity continued further into the afternoon and mating activity started earlier and lasted later into the day. Pollen-collecting activity occurred throughout the periods of observation on 22 May and 20 June. During the period of observation on 4 August no pollen-laden females were observed although two females captured and released had pollinia on their legs indicating that they had been taking nectar from a milkweed. Pollen from at least three species (yet to be determined) of plants has been collected from a series of females that were captured and released.

Xylocopa tabaniformis orpifex

In contrast to other subspecies of *X. tabaniformis*, *X. t. orpifex* is diurnal (O'Brien and Hurd, 1965). I have observed this bee for brief periods of time at Allen Springs, Yosemite National Park between 4,500 to 5,500 feet and in the San Bernardino Mountains between 5,500 and 6,500 feet. The first location is in the North Coast Ranges, the second in the Sierra Nevada, and the last in southern California.

In all locations females were active till late in the day (1800 hours). In the San Bernardino Mountains males also were active till this late hour. In Lake County activity started as early as 0700 hours. No hovering activity was observed at Allen Springs. During the morning hours there seemed to be a constant coming and going on the part of the male bees, although they were never seen to enter the same entrances used by the females. During the afternoon they were not observed as often as the females around the porch.

In Yosemite males flew from bush to bush of *Penstemon breviflorus* and *Eriodictyon californicum* (H. and A.) Torr. In southern California *Penstemon Grinnellii* Eastw. was patrolled in the same manner. Females were observed taking nectar from *Penstemon* flowers both in Yosemite and in southern California. At one location in the San Bernardino Mountains males had definite territories which included two or three bushes of *P. Grinnellii.* These males hovered, leg-dangled, and pursued other males in the same manner as reported for *X. c. californica.*

In San Bernardino County, once about 1730 hours and once about 1245 hours, I observed a male pounce on the back of a second bee which was taking nectar from a flower of *Penstemon Grinnellii.* I interpret this as possible mating behavior. In one instance the attacked bee was somewhat larger than the attacking male. In the second instance the bees actually fell out of the flower and onto the ground. The male, or aggressor, had grasped the second behind the wings so that its abdomen protruded beyond that of the feeding bee. In neither case was there a positive identification of the second bee as a female. In the first case the aggressor hovered behind the feeding bee before pouncing on it. This latter behavior was much like that described above for *X. c. californica.*

Both males and females spent a great amount of time collecting nectar from the *P. Grinnellii.* As much as 15 minutes were spent by an individual collecting nectar at a single plant. Judging from the rapidity of movement, males were just as effective as the females at gathering nectar. Nectar-collecting bees, except for the two mentioned above, remained unmolested by either patrolling males or other nectar-collecting individuals, whether male or female. As many as three females and two males were observed on the same plant at the same time.

In addition to the plants discussed above, females of *X. t. orpifex* have been observed to visit *Gilia capitata* Sims. for both nectar and pollen. Further, *Clarkia concinna* (F. and M.) Greene has been identified from a pollen load taken from a female at Allen Springs.

It is interesting that the females of both species of *Xylocopa* tend to enter the nests from a somewhat protected position. At Allen Springs I have never seen a female of *X. t. orpifex* enter one of the more exposed entrances, but always from beneath the porch. The majority of *X. c. californica* females seemed to enter their nests from beneath the porch rather than along the periphery of the porch. This, of course, keeps the females away from the hovering bees in the case of *X. c. californica*.

Finally, it is interesting that bees of the two species, although their nests are interspersed (see Fig. 2), never were seen to enter the wrong nest, with the exception of the nest in territory 12. This entrance was used by male *X. t. orpifex* and both male and female *X. c. californica*. Only males were observed to use the nests at 1, 2, 3, and 6; females used the nests at 4, 5, 10, and 11; and both males and females used the nests at 8 and 9. Males of *X. t. orpifex* used the nests along the periphery of the porch while the females used the entrances along the baseboard near territory 1 and an unindicated entrance in the corner opposite territory 3. *X. t. orpifex* nests were also found in the vertical timbers above the second story of the porch.

Acknowledgment

I wish to thank Dr. Paul Hurd, Jr. for his encouragement and suggestions during the period of the field observations and for his helpful review of the manuscript. This is one of a series of studies on carpenter bees made possible by a grant to Dr. Hurd from the National Science Foundation (NSF GB-2973, "Carpenter Bees of the World").

Literature Cited

Hurd, P. D., Jr. 1958. Observations on the nesting habits of some New World carpenter bees with remarks on their importance in the problem of species formation. Ann. Entomol. Soc. Amer., 51 (4): 365–375, 5 figs.

Hurd, P. D., Jr., and J. S. Moure, C.M.F. 1963. A classification of the large carpenter bees (Xylocopini). Univ. Calif. Publ. Entomol., 29: vi + 365 p., 1 frontis., 244 figs.

Janzen, D. H. 1964. Notes on the behavior of four subspecies of the carpenter bee, *Xylocopa* (*Notoxylocopa*) *tabaniformis* in Mexico. Ann. Entomol. Soc. Amer., 57 (3): 296–301, 2 figs.

O'Brien, L. B., and P. D. Hurd, Jr. 1965. Carpenter bees of the subgenus *Notoxylocopa*. Ann. Entomol. Soc. Amer., 58 (2): 175–196, 38 figs.